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Status of Land Birds on Selected Islands in the Ha'apai Group, Kingdom of Tonga[1]

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ABSTRACT: Based on fieldwork in 1995 and 1996, I assess the distribution, relative abundance, and habitat requirements of indigenous species of land birds on 13 islands in the Ha'apai Group, Kingdom of Tonga. Among the islands visited, primary forest still exists only on the large (46.6 km^2), high (558 m) volcanic island of Tofua. Vegetation on the 12 smaller (0.15–13.3 km^2), lower (6–45 m) islands is dominated by a mosaic of active and abandoned agricultural plots, nearly all with an overstory of coconut trees. Because of cultivation practices, very little of this vegetation is reverting to secondary forest. Of the 15 resident species of land birds that survive on these islands, nine are widespread and at least locally common within Ha'apai, although only four (*Gallirallus philippensis, Ptilinopus porphyraceus, Halcyon chloris, Aplonis tabuensis*) certainly or probably occur nowadays on all 13 islands. Three species (*Gallicolumba stairii, Ptilinopus perousii, Clytorhynchus vitiensis*) are extirpated or extremely rare on all islands surveyed except Tofua. Overall species richness and abundance of land birds are much greater on Tofua than on the other islands. This difference may be due more to the presence of primary forest on Tofua than to Tofua's greater area and elevation.

THIS PAPER DESCRIBES the current status of native land birds on 13 islands in the Ha'apai Group, Kingdom of Tonga. The field research was conducted to fulfill two goals: first, to describe long-term (prehistoric versus modern) changes in the distribution of each species; and second, to assess the relative abundance and habitat relationships of each species to provide information for conservation programs. The first goal includes studying bird bones from archaeological sites and is the focus of another publication. Here I emphasize the second goal.

Tonga is part of the West Polynesian avifaunal region that comprises Niue, Samoa, Wallis and Futuna, Fiji, and Rotuma (Watling 1982, Steadman 1993, 1997b). The extant, indigenous land birds of Tonga represent 17 genera (none endemic) and 18 species (two endemic). The birds of Ha'apai are not well known. They are treated in a general way in regional books, such as duPont (1976), Watling (1982), and Pratt et al. (1987). In spite of accounts of selected species on certain islands (Gill 1988, Rinke et al. 1992), meaningful lists of species (sensu Remsen 1994) were not available for any individual island in Ha'apai before this study, nor had relative abundances been estimated.

STUDY AREA

Physical Setting

The Ha'apai Group is the middle cluster of islands in the Kingdom of Tonga (Figure 1). The 62 islands within Ha'apai (Figure 2; many of the smallest islands not depicted) consist of five volcanic outliers to the west (Kao, Tofua, Falcon, Hunga Tonga, and

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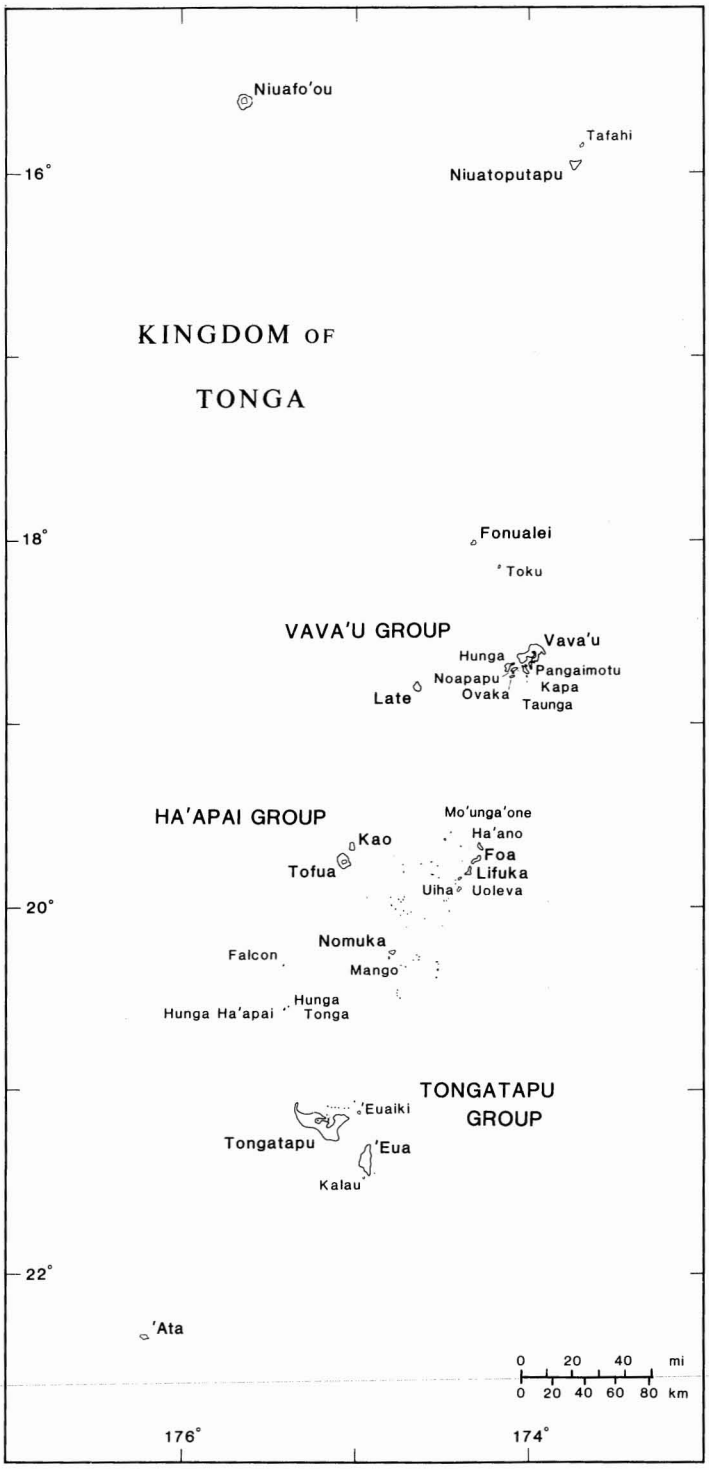

FIGURE 1. The Kingdom of Tonga.

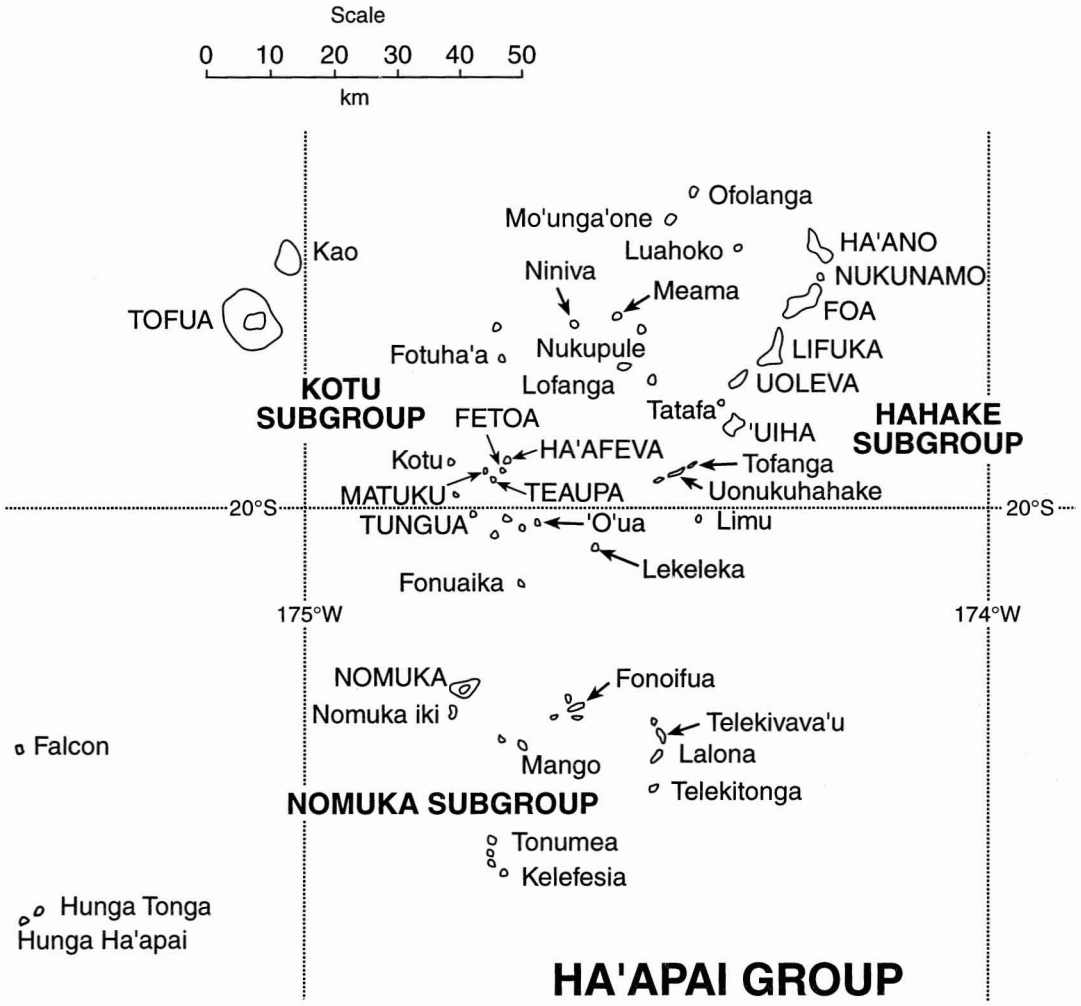

FIGURE 2. Ha'apai Group, Tonga. Islands surveyed are named in capital letters.

Hunga Ha'apai) and 57 raised limestone islands or sand cays. Based on their tectonic setting, the nonvolcanic islands are divided into three subgroups (Dickinson et al. 1994): 1, Hahake (Ha'ano, Nukunamo, Foa, Lifuka, Uoleva, Tatafa, 'Uiha); 2, Kotu (central Ha'apai); and 3, Nomuka (Nomuka and nearby southern islands). Rich archaeological sites, especially in the Hahake Subgroup, indicate that people have lived in Ha'apai continuously for the past 2800–3000 years (Dye 1990, Dye and Steadman 1990, Burley 1994, Burley et al. 1995, Dickinson et al. 1994). The human population of Ha'apai was about 9000 persons in 1993 (Christopher 1994).

The largest island in Ha'apai is Tofua (46.6 km^2), and the highest is Kao (1046 m). Among the 57 raised limestone islands and sand cays, the largest are Foa and Lifuka (Table 1), with 10 others (six of which I surveyed) having land areas >1 km^2. Most of the nonvolcanic islands are <20 m in elevation, although several are higher, such as Mango (38 m), Nomuka (45 m), and Fotuha'a (60 m).

TABLE 1

ISLANDS VISITED IN HA'APAI IN 1995–1996

SUBGROUP	ISLAND	AREA (km^2)	MAXIMUM ELEVATION (m)	HUMAN POPULATION[a]	DATES VISITED
Volcanic	Tofua	46.6	558	89	15–17 July 1995
Hahake	Foa	13.3	20	1,409	11, 23, 24 July 1996
	Lifuka	11.4	16	2,840	9–15, 23–26 July 1996
	Ha'ano	6.6	12	728	12 July 1996
	'Uiha	5.3	11	913	13 July 1996
	Uoleva	2.0	8	0	25 July 1996
	Nukunamo	0.25	6	0	12 July 1996
Kotu	Ha'afeva	1.8	10	449	17–22 July 1996
	Tungua	1.5	17	305	19 July 1996
	Matuku	0.3	11	142	20 July 1996
	Fetoa	0.15	16	0	20 July 1996
	Teaupa	0.15	17	0	20 July 1996
Nomuka	Nomuka	7.0	45	687	15–17 July 1996

[a] From the 1986 Tongan census.

The only long-term climate and weather data for Ha'apai are from Lifuka (Thompson 1986), where the mean daily minimum and maximum temperatures range from 23.9° and 29.8°C in February to 19.7° and 25.5°C in August. Of the 1805 mm mean annual rainfall, 67% occurs from November through April. The wettest months are March (253 mm, range 53–593) and April (288 mm, range 31–436). The driest months are June (74 mm, range 5–187) and July (90 mm, range 2–238). Ha'apai lies within the South Pacific trade wind zone, with east or southeast winds 60–70% of the time regardless of season.

Habitats

Except on certain low sand cays such as Nukunamo and Uoleva, the nonvolcanic islands in Ha'apai are covered with up to 8 m of volcanic tephra from eruptions on Tofua. The tephras have weathered into rich soils. It is not surprising, therefore, that the native vegetation has been altered for millennia by cutting and burning associated with agriculture. On none of the 12 nonvolcanic islands surveyed does even a small patch of mature forest still exist. The vegetation consists instead of a mosaic of active and abandoned agricultural plantations.

Crops grown in Ha'apai are dominated by species introduced or managed prehistorically in West Polynesia, such as breadfruit (*Artocarpus altilis*), paper mulberry (*Broussonetia papyrifera*), kava (*Piper methysticum*), Tahitian chestnut (*Inocarpus fagifer*), sweet potato (*Ipomoea batatas*), ti (*Cordyline fruticosum*), yams (*Dioscorea* spp.), sugar cane (*Saccharum officinarum*), coconut (*Cocos nucifera*), kape (*Alocasia macrorrhiza*), taro (*Colocasia esculenta*), pandanus (*Pandanus* spp.), and bananas (*Eumusa* spp., *Australimusa* spp.) (sequence and nomenclature follow Kirch [1994]). Modern crops also include species introduced to Polynesia within the past 200 yr, such as mango (*Mangifera indica*), various citrus (*Citrus* sp.), manioc (*Manihot esculenta*), papaya (*Carica papaya*), pineapple (*Ananas comosus*), and tannia taro (*Xanthosoma sagittifolium*). Woody but weedy exotics include *Adenanthera pavonina* and *Mimosa pudica.* The ubiquitous tall coconut trees reflect a former copra industry; today the coconuts are consumed locally (Perminow 1993). Coconut and pandanus are indigenous to Tonga and are actively managed to provide food, leaves for matting, fibers for cordage, and many other useful products. After coconut, mango is the next most common large tree in the

plantations. Tahitian chestnut is common on islands with wetlands.

Native woody species reoccupy abandoned plantations after some years, but in nonvolcanic Ha'apai the land usually is cleared again within ca. 5 to 30 yr, thereby not allowing the native species to grow into a canopied secondary forest. Instead, these trees tend to occur as scattered individuals or small groups, seldom with stem diameters >40 cm. Aside from coconut and pandanus, I noted the following native woody species in upland situations on one or more islands in nonvolcanic Ha'apai (sequence and nomenclature follow Drake et al. [1996]): *Cycas rumphii, Rhus taitensis, Cerbera odollam, Maniltoa grandiflora, Diospyros elliptica, Macaranga harveyana, Xylosma simulans, Hibiscus tiliaceus, Ficus obliqua, F. prolixa, F. tinctoria, Pisonia grandis, Jasminum didymum, Alphitonia zizyphoides, Morinda citrifolia, Santalum yasi, Elattostachys falcata, Grewia crenata,* and *Pipturus argenteus.* This list and the next one are not complete; they would be increased by proper botanical surveys, such as those of Sykes (1981) or Ellison (1990).

A degraded coastal forest forms a narrow perimeter (10–40 m wide) around most nonvolcanic islands in Ha'apai. Influenced by salt spray, this secondary forest is taller and richer in woody species on leeward than on windward coasts, although much of the leeward forest has been lost to village sites. Species of native trees often dominate the coastal perimeters and include *Cerbera odollam, Neisosperma oppositifolium, Barringtonia asiatica, Tournefortia argentea, Cordia subcordata, Casuarina equisetifolia, Calophyllum inophyllum, Terminalia cattapa, Xylocarpus moluccensis* (local in wetlands), *Macaranga harveyana, Scaevola sericea, Hernandia nymphaeifolia, Pemphis acidula, Hibiscus tiliaceus, Thespesia populnea, Acacia simplex, Ficus scabra, Pisonia grandis, Jasminum didymum, Colubrina asiatica, Bikkia tetrandra, Guettarda speciosa, Santalum yasi, Suriana maritima, Grewia crenata,* and *Pipturus argenteus.* No bird surveys were conducted exclusively in coastal forest, a habitat where birds are scarce today throughout Polynesia, regardless of the quality or extent of the upland forests. This scarcity is due primarily to a paucity of food because the dominant trees in coastal forest have large, bouyant, seaborne seeds or fruits (Straatmans 1964).

Tofua is a steep, active volcano that features a caldera lake of ca. 7 km^2 (Bauer 1970, Bryan et al. 1972). My entire time on Tofua was spent within or at the lakeside edge of mature forest inside the caldera. Virtually monospecific woodlands of *Casuarina equisetifolia* cover the immediate vicinity of the volcanic activity (similar plant communities are described for Niuafo'ou and Late Islands by Uhe [1974] and Sykes [1981]). Within 10–100 m of the lake's unstable edge, the following successional woody species occur: *Casuarina equisetifolia, Macaranga harveyana, Geniostoma* sp., *Hibiscus tiliaceus,* and *Morinda citrifolia.* All six stations on my survey transect were well within the rich mature forest, at least 1.0 km from the depauperate woodlands just described. The mature forest sustains numerous huge trees (diameters >2 m, canopy >25 m high), a very incomplete list of which includes *Rhus taitensis, Calophyllum neo-ebudicum, Diospyros* sp., *Elaeocarpus tonganus, Cryptocarya* sp., *Fagraea berteroana, Dysoxylum* sp., *Vavaea amicorum, Ficus obliqua, Myristica hypargyraea, Litsea mellifera, Syzygium* sp., *Pandanus tectorius, Alphitonia zizyphoides,* and *Micromelum minutum,* with *Calophyllum neo-ebudicum* and *Myristica hypargyraea* locally dominant. I saw no evidence of anthropogenic disturbance of forest inside the caldera rim. Deforestation on Tofua is limited to the outer slopes, associated with cultivation of kava (Perminow 1993).

MATERIALS AND METHODS

I surveyed birds on 12 islands in Ha'apai during 9–26 July 1996, as well as on Tofua during 15–17 July 1995 (Table 1). To estimate relative abundances of species, I conducted systematic surveys that consisted of point counts along transects. Records also were kept of all bird observations, regardless of the time of day. All transect data were

TABLE 2

BIRD TRANSECT DATA, HA'APAI, TONGA

ISLAND	DATE	TIME	NUMBER OF STATIONS			
			MATURE FOREST	SECONDARY FOREST	PLANTATION	TOTAL
Tofua	16 July 1995	0720–0844	6	—	—	6
Foa	23 July 1996	0905–1022	—	—	13	13
	24 July 1996	0705–1026	—	19[a]	12	31
Lifuka	10 July 1996	0725–0938	—	—	21	21
	11 July 1996	0700–0938	—	—	21	21
	26 July 1996	0709–0802	—	—	9	9
Ha'ano	12 July 1996	0815–1104	—	—	20	20
'Uiha	13 July 1996	0842–1024	—	—	16	16
Uoleva	25 July 1996	0729–0928	—	—	20	20
Ha'afeva	18 July 1996	0703–0958	—	—	27	27
	20 July 1996	0719–0918	—	—	15	15
Tungua	19 July 1996	0755–1044	—	—	27	27
Nomuka	16 July 1996	0706–0959	—	—	29[b]	29
	17 July 1996	0703–0926	—	—	24[c]	24
Total			6	19	254	279

[a] Includes two stations mixed with freshwater wetlands.
[b] Includes seven stations mixed with secondary coastal forest and two stations at the village edge.
[c] Includes 13 stations mixed with secondary coastal forest.

collected between 0700 and 1104 hours (Table 2). Surveys were not conducted during rainy or windy conditions. The locations of transects were recorded on topographic maps, copies of which are available from me. Aquatic species, such as herons, ducks, and migrant shorebirds, as well as seabirds flying overhead, were excluded from the analyses.

At each station along the transect I recorded each bird seen or heard within a 50-m radius during a 5-min period. Birds seen or heard at distances >50 m were noted but not included in the analyzed data. Stations were 100 m apart, whenever possible along a trail or one-lane dirt road to facilitate rapid but quiet travel between stations (Ralph et al. 1993). Individual birds recorded at the previous station were monitored during travel between stations and were not counted twice. Individual birds were recorded as being heard or seen.

Two measures of relative abundance were calculated for each species on each island. The first was "birds per station," which simply is the mean number of birds seen or heard per station, regardless of age, sex, or vocalization. The second was "pairs per station," which is the mean number of pairs of adult birds, a value that often is difficult to determine in tropical habitats where breeding seasons, group size, and territoriality may vary considerably among species. To convert the raw data from point counts for each species (presented as "birds per station" in Tables 3 and 5) into values that more accurately reflect the numbers of pairs present ("pairs per station" in Tables 3 and 4), I eliminated up to three individual birds seen but not heard at a station if another of its species was heard at the same station. Two to four birds seen together in a group were counted as one pair regardless of how many were vocalizing. This was important for species in which females and immatures are apparently as conspicuous as adult males, such as *Halcyon chloris, Lalage maculosa,* and especially *Foulehaio carunculata* and *Aplonis tabuensis.*

The scientific, English, and Tongan names for each species are given in the Species Accounts. J. J. Lister collected birds on Nomu-

TABLE 3

RELATIVE ABUNDANCES OF BIRDS IN FOREST TRANSECTS, HA'APAI, TONGA
(SEE MATERIALS AND METHODS FOR CALCULATIONS OF $\bar{X}$ PAIRS AND $\bar{X}$ BIRDS)

	$\bar{X}$ PAIRS PER STATION		$\bar{X}$ BIRDS PER STATION	
SPECIES	TOFUA	FOA	TOFUA	FOA
Circus approximans	—	0.05	—	0.05
Ptilinopus porphyraceus	1.00	1.58	1.00	1.58
Ptilinopus perousii	0.17	—	0.17	—
Ducula pacifica	2.33	—	4.33	—
Collocalia spodiopygia	0.50	—	0.83	—
Halcyon chloris	0.67	0.42	0.83	0.42
Lalage maculosa	—	0.53	—	0.79
Clytorhynchus vitiensis	1.17	—	2.33	—
Foulehaio carunculata	2.17	—	4.83	—
Aplonis tabuensis	1.17	0.84	2.67	1.16
Total species	8	5	8	5
Total $\bar{X}$ pairs/birds	9.17	3.42	17.00	4.00

TABLE 4

RELATIVE ABUNDANCES OF BIRDS ($\bar{X}$ PAIRS PER STATION) IN PLANTATION TRANSECTS, HA'APAI, TONGA
(SEE MATERIALS AND METHODS FOR CALCULATION OF $\bar{X}$ PAIRS)

SPECIES[a]	FOA	LIFUKA	HA'ANO	'UIHA	UOLEVA	HA'AFEVA	TUNGUA	NOMUKA	MEAN
Circus approximans	—	—	—	—	—	—	—	0.02	<0.01
Gallus gallus (i)	—	0.24	0.25	0.38	0.15	0.33	0.04	0.32	0.21
Gallirallus philippensis	—	0.18	0.10	0.50	—	0.07	0.07	—	0.12
Porphyrio porphyrio	—	0.04	—	—	—	0.02	—	0.02	0.01
Ptilinopus porphyraceus	0.68	0.43	0.80	0.56	0.20	0.62	0.33	0.23	0.48
Ducula pacifica	—	0.02	—	—	—	—	—	—	<0.01
Vini australis	—	—	—	—	—	0.50	0.52	—	0.13
Eudynamis taitensis (m)	—	0.04	0.05	—	0.05	—	—	—	0.02
Halcyon chloris	0.44	0.26	0.65	0.50	0.20	0.38	0.26	0.30	0.37
Hirundo tahitica	—	—	—	—	—	—	—	0.07	0.01
Lalage maculosa	0.84	0.20	0.05	0.06	0.05	—	—	0.08	0.16
Foulehaio carunculata	—	0.16	—	0.31	—	0.88	1.22	0.36	0.36
Aplonis tabuensis	0.92	0.92	0.95	0.82	0.75	0.64	0.26	0.40	0.71
Total species	4	8	5	6	4	7	6	8	6.0
Total $\bar{X}$ pairs	2.88	2.21	2.55	2.75	1.20	3.12	2.70	1.49	2.33

[a] i, introduced species; m, migrant species. i, m are not included in totals.

ka'iki in October 1889. C. H. Townsend collected birds on Nomuka in 1899 (Townsend and Wetmore 1919). The Whitney South Seas Expedition (WSSE) visited Ha'apai in 1925. The WSSE and other specimen localities are given for each species, considering only those islands that I visited as well.

RESULTS

The transect data (Tables 3–5) reveal major interisland differences in the presence and/or abundance of various species. The overall species richness and relative abundance of land birds are greater on Tofua than

TABLE 5

RELATIVE ABUNDANCES OF BIRDS ($\bar{X}$ BIRDS PER STATION) IN PLANTATION TRANSECTS, HA'APAI, TONGA (SEE MATERIALS AND METHODS FOR CALCULATION OF $\bar{X}$ BIRDS)

SPECIES[a]	FOA	LIFUKA	HA'ANO	'UIHA	UOLEVA	HA'AFEVA	TUNGUA	NOMUKA	MEAN
Circus approximans	—	—	—	—	—	—	—	0.02	<0.01
Gallus gallus (i)	—	0.24	0.25	0.38	0.15	0.04	0.52	0.74	0.29
Gallirallus philippensis	—	0.20	0.10	0.56	—	0.07	0.10	—	0.13
Porphyrio porphyrio	—	0.04	—	—	—	—	0.02	0.02	0.01
Ptilinopus porphyraceus	0.68	0.45	0.80	0.56	0.20	0.33	0.62	0.23	0.48
Ducula pacifica	—	0.04	—	—	—	—	—	—	<0.01
Vini australis	—	—	—	—	—	0.56	0.52	—	0.14
Eudynamis taitensis (m)	—	0.04	0.05	—	0.05	—	—	—	0.02
Halcyon chloris	0.44	0.27	0.80	0.50	0.20	0.26	0.43	0.34	0.38
Hirundo tahitica	—	—	—	—	—	—	—	0.07	0.01
Lalage maculosa	0.92	0.24	0.05	0.06	0.05	—	—	0.10	0.18
Foulehaio carunculata	—	0.20	—	0.31	—	3.07	1.24	0.38	0.65
Aplonis tabuensis	1.40	1.63	1.85	1.32	1.00	0.33	0.81	0.62	1.12
Total species	4	8	5	6	4	6	7	8	6.0
Total $\bar{X}$ birds	3.44	3.08	3.65	3.31	1.45	4.67	3.74	1.75	3.14

[a] i, introduced species; m, migrant species. i, m are not included in totals.

on the other islands (Table 6, Figure 3). The difference in relative abundance is particularly striking, with Tofua having 2.7 times more pairs and 3.6 times more individual birds than the next highest values. Logistical difficulties, including the lack of roads or trails, prevented me from doing point counts at more than six stations on Tofua. Nevertheless, the results from this small sample were corroborated by the abundant bird activity during the time I spent in Tofua's forests in the late morning and afternoon.

Birds are scarcest on Uoleva (a sand cay lacking tephra-derived soils) and Nomuka (a large, raised limestone island with tephra soils). Why these two islands support lower densities of birds than other nonvolcanic islands is not obvious. Very little agriculture is practiced today on Uoleva, where second-growth native trees are more common than on the inhabited islands of the Hahake Subgroup. Nomuka is intensively farmed, but not to any apparently greater extent than other inhabited islands. A possible factor on Nomuka is the negative influence of coastal forest at some stations.

Among the 15 indigenous species of resident land birds that survive on the 13 islands, nine are widespread and at least locally common within Ha'apai. Of these nine species, however, only four (*Gallirallus philippensis, Ptilinopus porphyraceus, Halcyon chloris, Aplonis tabuensis*) certainly or probably occur on all islands. These four most widespread species make up 71% of the pairs and 67% of the total birds in plantation transects compared with only 31% and 26%, respectively, in the mature forest transect on Tofua (Tables 3–5).

Of the seven species recorded on only one to four islands (Table 6), two (*Hirundo tahitica* and, to some extent, *Circus approximans*) prefer to forage near freshwater or brackish wetlands, the local nature of which probably restricts their distribution in Ha'apai. *Collocalia spodiopygia* requires caves or rock-shelters for roosting and nesting; such features are absent on all islands surveyed except Tofua and Nomuka. The three remaining species (*Gallicolumba stairii, Ptilinopus perousii, Clytorhynchus vitiensis*) are extirpated or rare on all nonvolcanic islands surveyed. These species seem to require mature forest, although *P. perousii* can exist in limited numbers without mature forest if large *Ficus* trees are available.

TABLE 6

SUMMARY OF LAND BIRD STATUS, HA'APAI, TONGA

SPECIES	TOFUA	FOA	LIFUKA	HA'ANO	'UIHA	UOLEVA	NUKUNAMO	HA'AFEVA	TUNGUA	MATUKU	FETOA	TEAUPA	NOMUKA	TOTALS (X)	TOTALS (X + A)
Circus approximans	A	X	A*	A*	A*	B*	B*	B*	B*	—	—	—	X	2	3
Gallus gallus (i)	A	X	X	X	X	X	X	X	X	X	—	—	X	10	11
Gallirallus philippensis	A	X	X	X	X	A	A	X	X	A	A	A	A	6	13
Porphyrio porphyrio	A	A	X	A	A	A	A	X	A	X	B	B	X	4	11
Gallicolumba stairii	A	—	—	—	—	—	—	—	—	—	—	—	—	0	1
Ptilinopus porphyraceus	X	X	X	X	X	X	X	X	X	X	A	A	X	11	13
Ptilinopus perousii	X	B	X	B	B	—	—	—	—	—	—	—	—	2	2
Ducula pacifica	X	A*	X*	A*	A*	A*	A*	B*	B*	B*	B*	B*	B*	1	1
Vini australis	A	X	X	A	A	A	B	X	X	X	A	X	A	6	12
Eudynamis taitensis (m)	A*	A*	X*	X*	A*	X*	A*	A*	A*	A*	A*	A*	A*	—	—
Tyto alba	X	A	A	A	A	A	A	A	X	A	B	B	X	3	11
Collocalia spodiopygia	X	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Halcyon chloris	X	X	X	X	X	X	X	X	X	X	A	X	X	12	13
Hirundo tahitica	X	A	A*	A*	A*	A*	A*	X	A*	A*	A*	A*	X	3	4
Lalage maculosa	X	X	X	X	X	X	A	B	B	B	—	—	X	7	8
Clytorhynchus vitiensis	X	—	—	—	B	—	—	B	—	—	—	—	—	1	3
Foulehaio carunculata	X	A	X	A	X	B	B	X	X	X	A	X	X	8	11
Aplonis tabuensis	X	X	X	X	X	X	X	X	X	X	X	X	X	13	13
Total resident species															
X only	11	7	9	5	6	4	3	8	7	6	1	4	9		
X + A	16	11	10	9	9	8	6	9	8	8	6	6	11		

NOTE: X, recorded July 1995 or July 1996; A, not recorded in 1995–1996 but likely occurs; B, not recorded in 1995–1996 but possibly occurs; i, introduced species; m, migrant species; *, breeding unlikely. Designation of A and B is based on known habitat preference, detectability, and time spent on the island. i, m, X*, A*, B* are not included in totals.

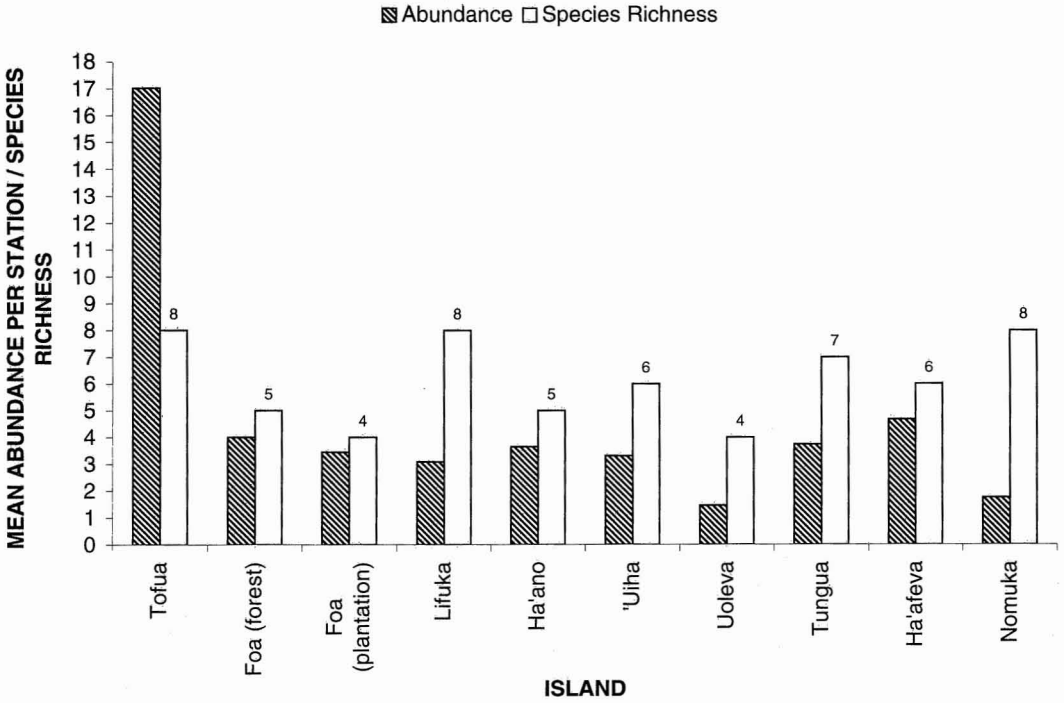

FIGURE 3. Relative abundance and species richness of land birds on surveyed islands in Ha'apai, Tonga. Based only on transect data in Tables 3, 5. See Table 6 for expanded species richness values. Data from Tofua are from forest. Data from Foa are from both forest and plantation. Data from all other islands are from plantation.

SPECIES ACCOUNTS

Circus approximans (Swamp Harrier, *taiseni*)

Outside Tofua (and perhaps Kao), the wetlands of Foa may be the only breeding locality within Ha'apai. Suitable nesting habitat (especially wetland margins) exists on Nomuka, although abundant human, canine, feline, and porcine activity may prevent nesting. This hawk probably visits any of the islands in Ha'apai occasionally. WSSE specimens: Tofua (Rinke et al. 1992).

Gallus gallus (Chicken, *moa*)

This nonnative gamebird was introduced prehistorically through most of Oceania including Tonga (Steadman 1993). *Gallus gallus* is abundant within villages in Ha'apai. Feral and semiferal birds occur irregularly in plantation lands, where they forage on the ground for seeds and invertebrates.

Gallirallus philippensis (Banded Rail, *veka*)

This terrestrial rail thrives in disturbed habitats, favoring thick grassy areas during the day and venturing into more open places to forage in the early morning and late afternoon. Because it does not vocalize reliably, the true relative abundance of *Gallirallus philippensis* probably is underestimated in my data. Two half-grown chicks were seen with two adults on Lifuka on 9 July. On 'Eua, Rinke (1987) reported eggs on 15 February, a newly hatched chick on 4 August, and a half-grown bird on 22 August.

Porphyrio porphyrio (Purple Swamphen, *kalae*)

This large rail is elusive on most Tongan islands, making survey difficult unless its distinctive (though often infrequent) vocalization is heard. *Porphyrio porphyrio,* like *Gallirallus philippensis,* thrives in agricultural

habitats. Unlike the latter, however, it also frequents wetlands of any size, preferably wooded. Thus islands such as Foa (where Gill [1988] recorded the species), Nomuka, and Ha'afeva probably sustain the core population of *P. porphyrio* in Ha'apai. Elsewhere in Tonga, large populations exist where predation from dogs and humans is minimal, such as on tiny Fafa Island (which lacks wetlands and is developed as a resort) off the north coast of Tongatapu or in the royally protected Ngofe Swamp on 'Uta Vava'u. A boy on Matuku killed an adult *P. porphyrio* in a leg snare on 20 July. This bird had an ovary 28 by 19 mm with many enlarged ova, light body molt, and worn, nonmolting remiges and rectrices. It measured as follows: culmen, 60 mm; wing, 224 mm; tail, 80 mm; and tarsus, 65 mm. The gizzard contained mashed greenery and black seeds 2 mm in diameter.

Gallicolumba stairii (West Polynesian Ground-Dove, *tu*)

A forest obligate in Tonga, *Gallicolumba stairii* often is difficult to see but is readily detected by its call (described by Beichle [1991]). I am confident that it no longer occurs on any of the nonvolcanic islands I visited in Ha'apai. Feral cats, which I recorded on every island in Ha'apai >1 km^2, are likely to have eliminated the populations of *G. stairii* that survived prehistoric human impact. Most Tongan farmers I questioned did not know the *tu;* those who did said that it was no longer (or never) found on their island but probably could still be found on Tofua. Given the current abundance of rats, cats, and pigs on Tofua, however, the long-term prospect for *G. stairii* there is not promising. Prehistoric bones document the extirpation of *G. stairii* on 'Eua and Lifuka (Steadman 1993, 1997b). Within Tonga today, *G. stairii* thrives only on Late and perhaps Hunga Ha'apai and Hunga Tonga (Rinke 1991). Holly Freifeld and I discovered a single population of *G. stairii* (six calling birds) in the Vava'u Group in 1995, in a relatively large remnant of mature forest at Mo'ungalafa on 'Uta Vava'u. This area is being cleared now for agriculture. WSSE specimens: Nomuka'iki, Hunga Ha'apai, Hunga Tonga, but none of the 13 islands I visited (Amadon 1943).

Ptilinopus porphyraceus (Purple-capped Fruit-Dove, *kulukulu*)

This frugivore is still common and widespread in Ha'apai, in part because it does not depend as exclusively as *Ptilinopus perousii* on the fruits of *Ficus obliqua.* On 'Eua, for example, 16 food plants are known for *P. porphyraceus* (Rinke 1987). This dove is more common in secondary or mature forest than in wooded plantation (Tables 3–5), an observation corroborated by data collected in Vava'u in 1995. Townsend specimen: Nomuka. WSSE specimens: Tofua, Ha'ano, Foa, Uoleva, 'Uiha, Ha'afeva, Tungua, Nomuka (Ripley and Birckhead 1942).

Ptilinopus perousii (Many-colored Fruit-Dove, *manuma'a*)

The call of *Ptilinopus perousii* is distinctive but delivered not as frequently or as loudly as that of *P. porphyraceus* (Rinke 1987, Engbring and Ramsey 1989, Beichle 1991; pers. obs.). I did not find this fig specialist on any transect on a nonvolcanic island. The only birds detected outside Tofua were in Pangai Village on Lifuka, where four pairs of *P. perousii* occupied two large *Ficus obliqua* trees (two pairs observed foraging in each tree, calling once every few minutes; none of the birds ever left these fig trees during an hour of observation). I counted 16 *F. obliqua* trees in Pangai, half of which bore ripe fruit in July 1996. Except for shoreline occurrences of *F. scabra,* very few individual trees of any species of *Ficus* occur outside villages in Ha'apai. The entire population of *P. perousii* on Lifuka probably is <30 birds. I encouraged local agriculture authorities to begin promoting *F. obliqua* (a strangling fig) around the islands, an undertaking that eventually would increase the food supply for all avian frugivores and may prevent the loss

of *P. perousii*. Gill (1988) also recorded *P. perousii* on Lifuka in July 1988. WSSE specimens: Tofua (Ripley and Birckhead 1942).

Ducula pacifica (Pacific Pigeon, *lupe*)

Abundant and conspicuous in the mature forest of Tofua, *Ducula pacifica* occurs on the nonvolcanic islands only as an occasional visitor. The sole individuals I detected during July 1996 were two birds flying low overhead just east of Pangai Village, Lifuka, on 26 July. Local men across Ha'apai consistently told me that the *lupe* is found regularly and in numbers only on Tofua and Kao. This large pigeon is hunted when it shows up on nonvolcanic islands, where numerous prehistoric pigeon mounds (*sia heu lupe*) attest to the former chiefly exploitation of *D. pacifica* (Burley 1996, Steadman 1997a). In spite of an excellent ("super-tramp") dispersal ability (Diamond 1974, Steadman 1997b), *D. pacifica* is unlikely to reestablish breeding populations on the nonvolcanic islands of Ha'apai because of the lack of indigenous forest (its preferred habitat [Franklin and Steadman 1991]), exacerbated by hunting pressure. WSSE specimens: Tofua (Amadon 1943).

Vini australis (Blue-throated Lorikeet, *henga*)

Except for interisland flights, every *Vini australis* that I observed or heard was either perched in or flying between coconut trees. This small parrot consumes nectar and pollen gathered with its brushy-tipped tongue. Given the abundance of coconut trees throughout nonvolcanic Ha'apai, poor-quality habitat seems unlikely to account for the scarcity of *V. australis* in the Hahake Subgroup. Differences in flowering phenology also seem unlikely to be a factor, because many coconut trees were in flower on each island. A possible influence on the current distribution of *V. australis* is which species of rat occurs on the island. Rinke (1985) suggested that *V. australis* is preyed upon more by *Rattus rattus* than by the smaller, less arboreal *R. exulans*. The island-by-island distribution of *R. rattus* versus *R. exulans* is unknown in Ha'apai. Another speculation for the striking interisland differences in abundance of *V. australis* (and perhaps another nectarivore, *Foulehaio carunculata*) might be the use of more pesticides in Hahake (and Nomuka?) than in Kotu. Although I have no information on pesticide use in Ha'apai, nontraditional (mechanized) agriculture is practiced more in the heavily populated Hahake Subgroup, where most of the farmers I questioned were unaware of the *henga*. Thrice on the afternoon of 20 July I saw pairs of *V. australis* approaching or leaving the northwest coast of Ha'afeva, flying about 20 m above the ocean. This small parrot is gone today from many of the West Polynesian islands that once were part of its range (Rinke 1985, Steadman 1993). WSSE specimens: Tofua, Uoleva, 'Uiha, Ha'afeva, Tungua (Amadon 1942*b*).

Eudynamis taitensis (Long-tailed Cuckoo, *karevareva*)

This migratory species breeds in New Zealand. During July (the austral winter) it was uncommon but regularly noted in any type of terrestrial habitat in Ha'apai. WSSE specimens: Nomuka (Bogert 1937).

Tyto alba (Common Barn-Owl, *lulu*)

Tongans across Ha'apai said that the *lulu* lived on their island. Nevertheless, I never saw or heard *Tyto alba* during frequent nighttime walks on various islands. The single bird on Tungua was flushed during a morning transect. Barn-owls were much more common (or at least more conspicuous) in Vava'u in July 1995 than in Ha'apai during July 1996.

Collocalia spodiopygia (White-rumped Swiftlet, *pekepeka*)

This small aerial insectivore is widespread and usually common on high islands in West Polynesia but is absent from most of Ha'apai because the islands are too low to have the

caves required for roosting and nesting. Caves are developed in the two isolated limestone outcrops on Nomuka, but to such a limited extent that the swiftlet population, if it ever existed, could have been eliminated easily by human activity.

Halcyon chloris (Collared Kingfisher, *sikota*)

Conspicuous on nearly every island surveyed, this habitat generalist feeds primarily on large insects and small lizards. In Vava'u it feeds regularly as well on small fish over the reef at low tide, a habit I observed only once in Ha'apai. Townsend specimen: Nomuka.

Hirundo tahitica (Pacific Swallow, *pekepeka*)

Common in nonvolcanic Ha'apai only near wetlands on Nomuka, *Hirundo tahitica* also was seen twice on Ha'afeva but not on transects. A large population lives near the lake on Tofua. This aerial insectivore feeds primarily near or over open water (fresh, brackish, or fringing reef). It visits other islands in Ha'apai, such as Lofanga (Gill 1988), Kelefesia, and Tonumea (Rinke et al. 1992). Lister and WSSE specimens: Nomuka'iki but none of the islands I visited. Townsend specimen: Nomuka.

Lalage maculosa (Polynesian Triller, *sikiviu*)

Among the nonvolcanic islands visited, this omnivorous gleaner was rare or absent except on Foa and Lifuka. I did not record *Foulehaio carunculata* on Foa, the only island where *Lalage maculosa* was common. Further, *F. carunculata* was abundant on the two islands larger than 1 km^2 (Ha'afeva, Tungua) where *L. maculosa* was not found (Tables 4, 5, Figure 4). Perhaps the aggressive *F. carunculata,* when so common in such a simplified habitat, somehow excludes the slightly

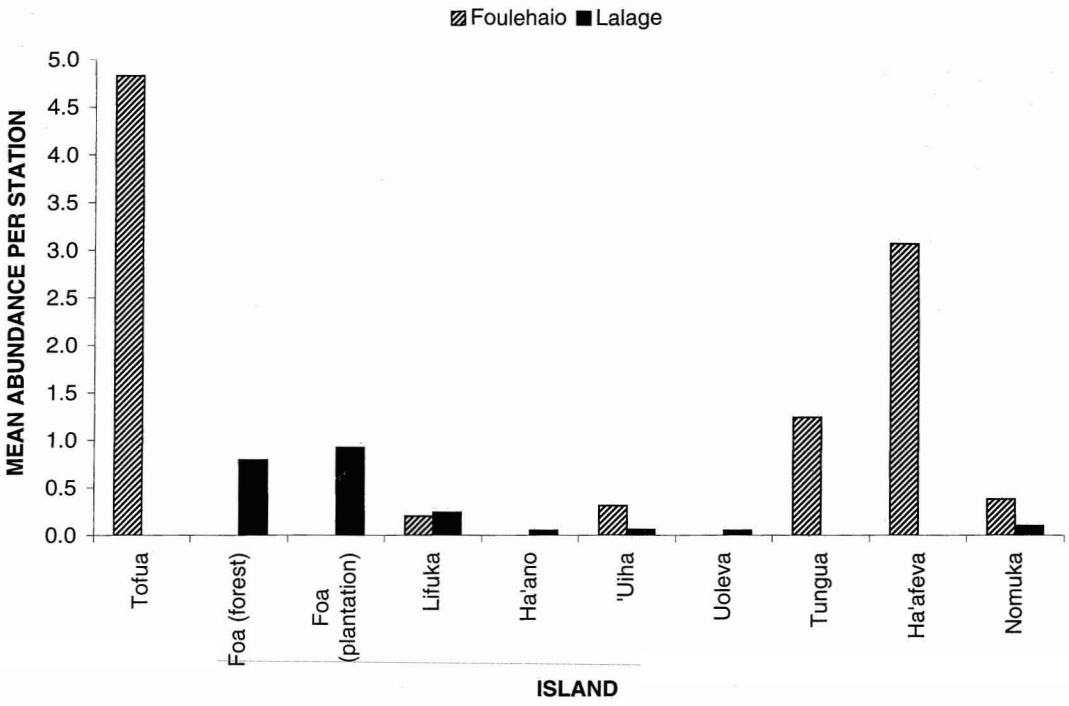

FIGURE 4. Relative abundance of *Lalage maculosa* versus *Foulehaio carunculata* on surveyed islands in Ha'apai, Tonga. Based on data in Tables 3, 5. Data from Tofua are from forest. Data from Foa are from both forest and plantation. Data from all other islands are from plantation.

smaller *L. maculosa.* In the mature forest of Tofua, *L. maculosa* was present but rare and was not recorded in the short transect. Townsend specimen: Nomuka. WSSE specimens: Tofua, Foa, Lifuka, Uoleva, Ha'afeva, Tungua, Nomuka (Mayr and Ripley 1941).

Clytorhynchus vitiensis (Fiji Shrikebill, *fuiva*)

This forest obligate is common and vocal on Tofua but may be gone from the nonvolcanic islands I visited in Ha'apai. I saw no habitat on those islands that seemed to be well suited for *Clytorhynchus vitiensis,* a gleaning insectivore/omnivore that forages mainly in the middle levels of forest but ranges from understory to canopy. On Ha'afeva, where it still occurred in 1991 (Rinke et al. 1992), *C. vitiensis* now seems to be gone. It was found on eight other small islands in the Nomuka Subgroup in 1991 (Rinke et al. 1992), none of which I visited. Farther south in Tonga, *C. vitiensis* survives as two small populations on the islets of 'Eueiki (off Tongatapu) and Kalau (off 'Eua), although it once occurred on both Tongatapu and 'Eua (Rinke 1987, Steadman 1993). It was not found on any of the 16 islands surveyed in Vava'u in 1995 and 1996 (pers. obs.). The small populations of *C. vitiensis* that may still exist on nonvolcanic islands in Ha'apai are vulnerable to extinction, probably within years or decades. Townsend specimen: Nomuka. WSSE specimens: Tofua, Uoleva, Tungua, Teaupa (Mayr 1933).

Foulehaio carunculata (Wattled Honeyeater, *fuleheu*)

This noisy, conspicuous, aggressive nectarivore/insectivore occurs in groups of two to six birds (usually three or four). Tofua sustains the highest numbers of *Foulehaio carunculata* within the study area. In nonvolcanic Ha'apai, it seems to thrive on certain islands yet be nearly if not absolutely absent in similar habitats (coconut-dominated plantations) on other islands (Figure 4). Perhaps differences in pesticide use influence the relative abundance of *F. carunculata* in these simplified woodlands. This honeyeater is most often found in coconut trees, although breadfruit, mango, coral bean, and other flowering trees are used as well. Rinke (1984) listed 12 trees visited by *F. carunculata* on 'Eua. Townsend specimen: Nomuka. WSSE specimens: Tofua, Ha'ano, Uoleva, 'Uiha, Ha'afeva, Tungua, Teaupa, Nomuka (Mayr 1932).

Aplonis tabuensis (Polynesian Starling, *misi*)

This highly frugivorous omnivore is the most common bird in each plantation transect in Ha'apai except Ha'afeva and Tungua (Tables 4, 5). *Aplonis tabuensis* is common in forests as well (Table 3). It nests in snapped coconut trunks or beneath the dead fronds surrounding the upper trunk of a coconut, the latter also serving as a preferred nest site for *Vini australis.* The fruit consumed by *A. tabuensis* in Ha'apai includes native species (*Ficus* spp., *Grewia crenata, Rhus taitensis, Alphitonia zizyphoides, Cryptocarya* sp.) and nonnative species (*Carica papaya, Psidium guajava, Lantana camara*). Townsend specimen: Nomuka. WSSE specimens: Tofua, Ha'ano, Foa, Lifuka, Uoleva, 'Uiha, Ha'afeva, Tungua, Teaupa, Nomuka (Mayr 1942).

DISCUSSION AND CONCLUSIONS

The data and interpretations presented here could be bolstered by future transect surveys that target especially the numerous Tongan islands that remain unsurveyed. Also needed is more complete coverage of individual islands (more stations per island, especially on Tofua and other volcanic islands). Using standardized methods, these surveys are an efficient way to monitor bird populations. Mist-net surveys were done on Late by Rinke (1991), although capture data from mist-nets may not reliably indicate the relative abundance of birds (Remsen and Good 1996). Another deficiency in our knowledge of Tongan birds is the poor state of autecological information. Fundamental aspects of behavior and ecology are unknown or poorly

TABLE 7

SELECTED FACTORS THAT INFLUENCE DISTRIBUTION AND POPULATION SIZE FOR INDIGENOUS, RESIDENT LAND BIRDS IN HA'APAI, TONGA

SPECIES	INTERISLAND DISPERSAL ABILITY	ABILITY TO WITHSTAND DEFORESTATION	ABILITY TO WITHSTAND NONNATIVE PREDATORS	MAXIMUM POPULATION DENSITY	TOTAL
Circus approximans	3	3	2	1	9
Gallirallus philippensis	3	3	2	2	10
Porphyrio porphyrio	3	3	2	1	9
Gallicolumba stairii	1	1	1	0	3
Ptilinopus porphyraceus	3	2	2	3	10
Ptilinopus perousii	1	2	2	0	5
Ducula pacifica	3	2	1	1	7
Vini australis	3	3	2	2	10
Tyto alba	3	3	2	0	8
Collocalia spodiopygia	3	3	3	0	9
Halcyon chloris	3	3	3	2	11
Hirundo tahitica	3	3	3	1	10
Lalage maculosa	2	2	2	2	8
Clytorhynchus vitiensis	1	1	2	0	4
Foulehaio carunculata	2	2	3	3	10
Aplonis tabuensis	3	3	3	3	12

NOTE: 1, low; 2, medium; 3, high. These values are impressionistic and arbitrary. Lower scores mean less resistance to population decline or extirpation. Nonnative predators consist of humans, rats, cats, dogs, and pigs. Values for maximum population density are confined to the 12 nonvolcanic islands (mean birds rather than mean pairs [Tables 3–5]), with values assigned as follows: 0 for unrecorded species; 1 for <0.5; 2 for 0.5 to 1.0; and 3 for >1.0.

documented for most species. Only through detailed nesting and feeding studies of individual species can we better understand their role in Tonga's terrestrial ecosystems.

Within West Polynesia, transect surveys of land birds have been conducted in American Samoa (Amerson et al. 1982, Engbring and Ramsey 1989, American Samoa Government Department of Marine and Wildlife Resources 1995) and Western Samoa (Bellingham and Davis 1988). The survey in Western Samoa by Evans et al. (1992) was based on sightings only and thus is less useful in quantifying relative abundance. This paper reports the first transect survey of birds in Ha'apai and only the second such effort in all of Tonga. The other Tongan transect survey was conducted by Holly Freifeld and myself as part of a 2-month survey of forest vegetation and vertebrate communities in Vava'u in 1995, the results of which are being prepared separately for publication.

Influences on Presence/Absence and Relative Abundance

At least four factors, and perhaps two others, seem to affect the current status of land bird populations in Ha'apai: (1) the ability to disperse between islands; (2) tolerance to human-induced habitat changes, especially deforestation and cultivation; (3) ability to withstand predation by humans and other mammals (rats, cats, dogs, and pigs); (4) maximum population density; (5) tolerance to toxic chemicals; and (6) interactions (disease, competition, predation) with nonnative birds. Factors 1, 2, and 4 and to a lesser extent 3 have been evaluated partially through field observation. Factors 5 and 6 are more purely speculative.

Table 7 shows an evaluation of the first four factors, based on my field observations during a total of 21 weeks in Tonga in 1985, 1988, 1989, 1995, and 1996. These arbitrary

values are not additive in a strict mathematical sense, although higher total scores tend to reflect the more resistant (less vulnerable) species, and the three most localized species in Ha'apai have the lowest total scores.

A good ability to disperse between nearby islands allows populations to come and go as circumstances change on any one island. This dispersal is within Ha'apai, among islands within sight of each other. Factors 1 and 2 are not independent; species more strictly confined to mature forest tend to be poor dispersers, whether on oceanic islands or in the continental tropics. *Ducula pacifica* is an exception, being an excellent disperser over water that nevertheless requires forest cover. Rarity (related to factor 4) may affect this categorization of species; with all else equal, a rare species is less likely to be recorded crossing water than a common species. That this may not be a major influence, however, is suggested by the Tongan Whistler, *Pachycephala jacquinoti,* which was common on forested islands in Vava'u in 1995 but was never recorded over water on any of numerous interisland boat trips. Field observations of dispersal are, of course, so limited in time scale that they probably can detect dispersal only in species that commute over water in the course of their regular daily or seasonal activities. My observations almost certainly would fail to detect dispersal events that occur only once in a bird's lifetime, such as, perhaps, a juvenile Tongan Whistler crossing to an adjacent island.

Gallicolumba stairii, Ptilinopus perousii, and *Clytorhynchus vitiensis* are the three species in Ha'apai with the poorest interisland dispersal abilities (i.e., that I never have seen flying over the ocean anywhere in Tonga) and the strongest preference for mature forest. These three species already are gone or rare on most if not all nonvolcanic islands in Ha'apai. They are the residue of a once much larger set of forest-obligate Tongan species, most of which are extinct or no longer occur anywhere in Tonga (Steadman 1993, 1995).

West Polynesians have hunted birds for several thousand years (Craig et al. 1994, Steadman 1995, 1997a). Human hunting pressure (guns, snares, thrown rocks) is greatest in Ha'apai today for *Porphyrio porphyrio* and *Ducula pacifica. Gallirallus philippensis* and *Ptilinopus porphyraceus* are hunted regularly but to a lesser extent. The populations of other native land birds in Ha'apai sustain little human hunting. Even for the four species just mentioned, hunting may have little effect today on distribution or population size.

Maximum population density is considered a factor in overall distribution because, at least in theory, species with higher population densities on at least one island may provide a better source of emigrants than rare species and also be less likely to become extinct for stochastic reasons.

The nectar-feeders *Vini australis* and *Foulehaio carunculata* are scarce or absent on islands in the Hahake Subgroup, where I detected no peculiarities of habitat that would lead to reduced numbers of nectarivores. Coconut trees, the primary source of nectar, are abundant here as elsewhere in nonvolcanic Ha'apai. Two possible factors are interisland differences in the use of pesticides and in the distribution and abundance of *Rattus exulans* versus *R. rattus,* the latter being a more effective arboreal predator. *Foulehaio carunculata* is still locally common, however, on 'Eua and Tongatapu, two large islands with heavy pesticide use and huge populations of *R. rattus* (pers. obs.).

To review briefly the remaining species, *Tyto alba* is a habitat generalist of unknown abundance that is well supplied with its favored food, rats, in Ha'apai. Two insectivores are habitat generalists as well (*Halcyon chloris, Lalage maculosa*), whereas the distribution of *Collocalia spodiopygia* is confined by its requirement of caves for roosting and nesting. *Hirundo tahitica* is limited in distribution by its preference to forage and nest near freshwater lakes and rivers or mangrove estuaries. *Aplonis tabuensis* thrives because, at least in Tonga, it is a generalist in habitat and food habits, although its relative abundance is greater on Tofua than on any of the less-forested islands.

One species that might still exist in Ha'apai although I did not detect it is *Porzana tabuensis* (Sooty Crake, *moho*). Based on its habitat preference elsewhere in Polynesia (wetlands with abundant grasses, sedges, or other herbaceous growth [Franklin and Steadman 1991]), suitable habitat for *P. tabuensis* may exist today on Foa, Nomuka, and Ha'afeva. None of the farmers I spoke with, however, knew the *moho,* nor did I hear its call. This negative evidence is not definitive in the absence of using a tape recorder. Bones of *P. tabuensis* occur commonly in prehistoric sites on Lifuka and 'Eua, where wetlands are absent or very limited today (Steadman 1993; unpubl. data). WSSE specimens of *P. tabuensis* have been collected on Tongatapu, Hunga Ha'apai, Late, and Fonualei (Amadon 1942*a*).

Nonnative Species

Various combinations of nonnative mammals occur on each of the 13 islands visited. These include the prehistorically introduced Pacific rat (*Rattus exulans*), dog (*Canis familiaris*), and pig (*Sus scrofa*), as well as the historically introduced black rat (*Rattus rattus*), house cat (*Felis catus*), horse (*Equus caballus*), goat (*Capra hircus*), and cow (*Bos taurus*). The islands inhabited by people tend to have most if not all of these species.

The chicken is the only nonnative species of bird established in Ha'apai. This domesticate has lived in Ha'apai since human colonization (D. W. Steadman, A. M. Plourde, and D. V. Burley, unpubl. data). Ha'apai does not yet seem to have populations of four other nonnative species that are established now elsewhere in Tonga (Rinke 1986*a,b,* 1987, Gill 1987, 1988; pers. obs.): Rock Dove (*Columba livia*) on Tongatapu; Red-vented Bulbul (*Pycnonotus cafer*) on Tongatapu, Niuafo'ou, and locally on 'Uta Vava'u; European Starling (*Sturnus vulgaris*) on Tongatapu and 'Eua (two individuals of *S. vulgaris* were observed on Foa by Gill on 13 July 1988; I did not see *S. vulgaris* anywhere in Ha'apai in 1996); and Jungle Myna (*Acridotheres fuscus*) on Niuafo'ou. If any of these species are discovered in Ha'apai, the population should be eradicated before it becomes established.

Interactions between native and nonnative birds have not been studied much in Tonga. In Tonga's capital of Nuku'alofa, the nonnative *Pycnonotus cafer* and *Sturnus vulgaris* are now the two most common species. This may apply for all of Tongatapu, the largest island (325 km^2) in Tonga. Unless the spread of nonnative species is contained, this could be the eventual fate of other Tongan islands as well.

Importance of Forested Volcanic Islands

That the overall species richness and relative abundance of land birds on Tofua are greater than on the nonvolcanic islands probably is due more to the presence of mature forest on Tofua than to Tofua's larger land area and higher elevation. This conclusion is supported by two lines of evidence from Ha'apai's nonvolcanic islands: (1) the former residency of various extinct or extirpated species (indicated by prehistoric bones from three archaeological sites [see Steadman 1989, 1995, and Table 8 herein]); and (2) the greater species richness and relative abundance of land birds in secondary forest than in active or recently abandoned agricultural plots. This is documented on Foa (Tables 3–5) as well as in Western Samoa and the Cook Islands (Bellingham and Davis 1988, Franklin and Steadman 1991). The rugged coastline and steep, inhospitable terrain of Tofua (and other volcanic islands in Ha'apai) restrict human activity and thus act to preserve forest. If deforestation and agriculture were as pervasive on Tofua as on nonvolcanic islands in Ha'apai, the abundance of birds on Tofua probably would resemble that on the other islands.

This is not to imply that there has been no anthropogenic extinction of birds on Tofua. Although Tofua lacks prehistoric faunal data, I believe that any of the volant extinct species discovered on nonvolcanic islands in Ha'apai also used to occur on Tofua. The most vulnerable species (especially various megapodes, pigeons, and flightless rails) have been lost throughout Ha'apai, to unknown

TABLE 8

PREHISTORIC VERSUS MODERN RECORDS OF LAND BIRDS FROM THE ADJACENT ISLANDS OF FOA AND LIFUKA, HA'APAI GROUP, TONGA

SPECIES	PREHISTORIC	MODERN
Circus approximans Swamp Harrier, *taiseni*	—	X
†*Megapodius alimentum* Consumed Megapode	X	—
†*Megapodius molistructor* Giant Megapode	X	—
**Megapodius pritchardii* Niuafo'ou Megapode, *malau*	X	—
Gallus gallus (i) Chicken, *moa*	X	X
**Porzana tabuensis* Sooty Crake, *moho*	X	—
Gallirallus philippensis Banded Rail, *veka*	X	X
Gallirallus, undescribed sp. Lifuka Flightless Rail	X	—
Porphyrio porphyrio Purple Swamphen, *kalae*	X	X
**Gallicolumba stairii* West Polynesian Ground-Dove, *tu*	X	—
†*Didunculus*, undescribed sp. Large Tooth-billed Pigeon	X	—
†*Caloenas* cf. *canacorum* Large "Nicobar" Pigeon	X	—
Ptilinopus porphyraceus Purple-capped Fruit-Dove, *kulukulu*	X	X
Ptilinopus perousii Many-colored Fruit-Dove, *manuma'a*	X	X
Ducula pacifica Pacific Pigeon, *lupe*	X	X
**Ducula latrans* Peale's Pigeon	X	—
†*Ducula david* David's Pigeon	X	—
†*Ducula*, undescribed sp. Giant Pigeon	X	—
Vini australis Blue-throated Lorikeet, *henga*	—	X
**Prosopeia tabuensis* (i?) Musk-Parrot, *koki*	X	—
Eudynamis taitensis (m) Long-tailed Cuckoo, *karevareva*	X	X
Tyto alba Common Barn-Owl, *lulu*	X	X
Halcyon chloris Collared Kingfisher, *sikota*	X	X
**Halcyon* sp. (small) Small Kingfisher	X	—
Lalage maculosa Polynesian Triller, *sikiviu*	X	X
**Clytorhynchus vitiensis* Fiji Shrikebill, *fuiva*	X	—
Foulehaio carunculata Wattled Honeyeater, *fuleheu*	X	X
Aplonis tabuensis Polynesian Starling, *misi*	X	X
Total resident species	23	12

NOTE: Prehistoric records are from three early archaeological sites (Faleloa, Tongoleleka, and Holopeka [see Steadman 1989, unpubl. data; Burley 1994, Dickinson et al. 1994, Burley et al. 1995]). Many bones from these sites are yet to be studied. †, extinct species; *, extirpated on Foa and Lifuka but extant on one or more islands elsewhere in Tonga; i, introduced species; m, migratory species; i, m are not included in totals.

combinations of predation, habitat loss, and perhaps disease (Steadman 1995). The forested conditions on Tofua today allow many of Tonga's extant species to live in greater abundance than on the more degraded nonvolcanic islands. The extent to which Tofua was deforested prehistorically is not known.

Given the intense land use on most of the nonvolcanic islands today, Tofua is an essential island for conserving populations of birds, as pointed out by Rinke (1986*b*). Tofua probably sustains Ha'apai's largest remaining populations of *Circus approximans, Ptilinopus porphyraceus, P. perousii, Ducula pacifica, Clytorhynchus vitiensis, Foulehaio carunculata,* and *Aplonis tabuensis.* In light of how much extinction of birds already has occurred in Tonga (Steadman 1989, 1993, 1995), it seems appropriate to afford protection to the forests of Tofua (and adjacent Kao) as refuges for indigenous plants and wildlife.

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